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UNIVERSITY OF ALBERTA

LIGHT TRANSMISSION THROUGH BOREAL MIXEDWOOD STANDS

BY

ANNETTE J. CONSTABEL

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

DEPARTMENT OF FOREST SCIENCE

Edmonton, Alberta
SPRING 1995

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Dr. M.R.T. Dale

Date Jan. 31, 1995

Dedication

To my parents, who provided inspiration.

Abstract

Measurements of light transmission were made in spring, summer and autumn in three overstory types: young aspen (*Populus tremuloides* Michx.); old aspen; and mixed old aspen - white spruce (*Picea glauca* (Moench) Voss). The spring, with relatively high solar elevation angles and the least shading, showed the greatest light intensitites penetrating all understory levels in all overstory types. At ground level, low light intensities prevailed in the summer, suggesting that white spruce seedlings may rely on high light conditions during the spring, and also in the autumn in pure aspen stands, for a large portion of their annual carbon gain. In a second study, percent light transmission was measured through individual crowns of white spruce and aspen over a range of solar elevation angles. Overall, white spruce intercepted approximately six times as much light as aspen. For both tree species, light transmission increased with decreased solar elevation angle.

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Chapter I.

General Introduction and Literature Review

Advance regeneration (regeneration present before harvesting) of white spruce (*Picea glauca* (Moench) Voss) in the understory of boreal mixedwood stands is valuable to forest managers because it can decrease regeneration costs and the rotation time to the next harvest (Navratil *et al.* 1994, Froning 1980). Apart from seedbed and seed sources, the recruitment of white spruce advance regeneration likely relies on the amount of light transmitted to the forest floor. The ability to promote white spruce advance regeneration in sufficient quantities, would be of great benefit to managers who struggle to achieve present day stocking standards. While it is known how much light is necessary for white spruce growth in the understory (Brix 1972, Logan 1969), it is not known how much light is actually transmitted to the understory and forest floor of boreal mixedwood stands. Light transmission through boreal mixedwood stands is not constant, but changes with the structure of the over-and understory and with the angle of solar radiation.

The following is a discussion of the boreal mixedwoods, the factors that affect light transmission, and how light transmission can be measured.

The Boreal Mixedwoods

Boreal mixedwood forests (in this thesis defined as comprising of pure or mixed white spruce and aspen ecosystems) are found in the two Boreal-Cordilleran and three Boreal Mixedwood Ecoregions of Alberta which together comprise approximately 70 % of Alberta's landbase (Strong and Leggat 1992). The Boreal-Cordilleran Ecoregions represent a transition between the coniferous Subalpine Ecoregion to the west, and the largely deciduous Aspen Parkland

Ecoregion to the east (Strong and Leggat 1992). The smaller Upper Boreal-Cordilleran (UBC) Ecoregion occupies the higher elevations in the Boreal-Cordilleran Ecoregion. The resulting cool climate in the UBC Ecoregion leads to dominance by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and the absence of deciduous tree species (Strong and Leggat 1992). The warmer Lower Boreal Ecoregion (LBC) is the most arboreally diverse area in Alberta (Strong and Leggat 1992). The tree species found include: aspen (*Populus tremuloides* (Michx.) Beauv.); balsam poplar (*Populus balsamifera* L.); paper birch (*Betula papyrifera* Marsh.); white spruce; black spruce (*Picea mariana* (Mill.) BSP.); balsam fir (*Abies balsamea* (L.) Mill.); lodgepole pine; and Jack pine (*Pinus banksiana* Lamb.). The LBC Ecoregion is the second largest ecoregion in Alberta, covering 93 061 km^2, or 14.1 % of Alberta's land area (Strong and Leggat 1992). It is considered to have the most favorable climate for white spruce growth in Alberta (Strong and Leggat 1992).

Patterns of succession in the boreal mixedwoods show initial dominance of disturbed sites by pioneering herbs, shrubs, and aspen, with ingress of more shade tolerant tree species such as white spruce, black spruce, or balsam fir. White spruce commonly grows beneath an aspen overstory for many years, but eventually outgrows the aspen overstory in height and age. Mature aspen dominated stands are found to have well-developed shrub and herb layers, whereas mature conifer dominated stands show extensive moss cover and poor herb and shrub layers (Peterson and Peterson 1992, Rowe 1956). Common shrubs associated with white spruce and aspen in west-central Alberta are: *Rosa acicularis* L.; *Viburnum edule* (Michx.) Raf.; *Lonicera involucrata* (Richards.) Banks; and *Sheperdia canadensis* (L.) Nutt. (Corns and Annas 1986). Common species in the herb layer are: *Cornus canadensis* L.; *Epilobium angustifolium* L.; *Aralia nudicaulis* L.; and *Calamagrostis canadensis* (Michx) Beauv. (Corns and Annas 1986). The common bryophytes found on the forest floor under white spruce

overstories are: *Hylocomium splendens* (Hedw.) B.S.G.; *Pleurozium schreberi* (Brid.) Nutt.; and *Ptilium crista-castrensis* (Corns and Annas 1986).

Light transmission through boreal mixedwood stands is thought to change substantially with overstory composition and cover, understory composition and cover, and season. A discussion of the effect of each of these factors follows:

Overstory Composition and Cover

Aspen Crowns

Pure stands of aspen reach maximum crown cover between 15 - 20 years of age, after which density changes little or decreases (Peterson and Peterson 1992). However, even in closed stands, aspen is considered to have a sparse crown (Peterson and Peterson 1992). Further, shaded leaves and branches naturally prune due to aspen's shade intolerance, resulting in short crowns (Peterson and Peterson 1992). A relatively large amount of incoming radiation passed through aspen dominated overstories to 1.3 m in a study by Lieffers and Stadt (1994). Aspen leaves also "tremble" or flutter due to flattened petioles that catch the wind. Wind causes rapid variation in the amount of radiation passing through a canopy at midday (Norman and Tanner 1969) and may further increase light transmission through aspen canopies.

White Spruce Crowns

White spruce shows strong apical dominance and poor self-pruning ability, producing long, densely foliated crowns. When found in mixed stands with aspen (which allows more side light to reach the crowns than in pure stands), live branches are retained almost to the forest floor. White spruce overstories intercepted much more incoming radiation than aspen overstories

based on measurements of light transmitted to 1.3 m in boreal mixedwood stands (Lieffers and Stadt 1994).

An increased proportion of white spruce in the overstory over time was shown to change understory composition and cover in the boreal forest (Ellis 1986). The measured changes in the understory were assumed to be due to decreasing light transmission with changing overstory composition. The amount and grouping of aspen to white spruce in the overstory is therefore an important characteristic in the attenuation of light in a mixedwood stand. Several methods may be used to estimate crown composition and cover.

Basal area

Basal area is the total cross sectional area of tree stems per hectare, calculated from tree diameters at 1.3 m (dbh). Basal area was not found to be a good predictor of crown biomass (cover) (Snell and Brown 1978) nor did overstory composition based on basal area predict light transmission in mixedwood stands (Lieffers and Stadt 1994). Lieffers and Stadt (1994) found light transmission to increase in aspen stands with increasing basal area, while the opposite held true in white spruce stands. In mixedwood stands, the aspen overstory generally grows as a pure layer, until white spruce or other conifers encroach dominant canopy positions when aspen are already beyond maturity. White spruce growing into an aspen overstory would receive more side light and would typically have a much longer live crown than those growing in pure stands. Basal area to crown cover ratios of white spruce derived in pure stands would therefore not provide good estimates for mixedwood stands.

Optical Estimates

Crown cover may be estimated by a number of optical techniques. Vales and Bunnell (1988) tested six common techniques on a variety of pure stands.

They found the size of the angle of view to be the most important difference between techniques. Unaided visual estimates, the gimbal sight (a viewfinder lens with crosshairs and a level) (Walters and Soos 1962), and the moosehorn (a sighting tube with 25 dots etched on it) (Robinson 1947) sample a narrow viewing angle. The spherical densiometer (a convex mirror with a grid of 24 squares etched on it) (Lemmon 1956) samples an approximately 60° view (Vales and Bunnell 1988) while hemispherical photographs using a "fisheye" lens capture a 180° view. Solar paths for different days may be traced on hemispherical photographs, and the area of foliar cover versus open sky measured on them. In general, the photographic method is used to make treatment comparisons, and to describe the radiation loads at specific sites. It seems less useful in describing stand level radiation regimes unless repeated many times over the stand.

Narrow angle techniques view a small horizontal portion of the crown directly overhead, while wide angle techniques record much of the depth of neighbouring crowns as well (Vales and Bunnell 1988). Vales and Bunnell (1988) found wide angle techniques to estimate greater crown cover with less variance than narrow angle techniques. Since incoming solar radiation is seldom directly overhead, the depth of crowns is an important feature in estimating the light environment in the understory. The effect of long narrow crowns, like those of white spruce, would be greatly underestimated with a narrow angle measuring technique. The range and variance of wide angle techniques are small because crown estimates cover a much greater area (Vales and Bunnell 1988). The authors also found that narrow angle techniques are more greatly affected by height to the base of the live crown than wide angle techniques. The likelihood of crowns being in the angle of view is decreased for shorter trees since the angle subtends a greater area the further it extends. This effect is heightened for narrow angles over wide angles, since wide angles will always cover much more area. Vales and Bunnell (1988) found the disparity

between wide and narrow technique estimates to decrease with increasing crown cover. A wide angle technique, rather than a narrow angle technique, is more appropriate for estimating the radiation environment in the understory due to the importance of a wide range of solar angles (Vales and Bunnell 1988) and is likely also more appropriate in sites at high latitudes where the sun is never directly overhead.

Crown cover techniques have been tested only in pure, even-aged stands. Finding crown cover in mixes of: tall and short trees; short and long crowned tree species; or coniferous and deciduous crowns, is more difficult. A narrow angle technique in a stand of both long and short crowned trees might provide an accurate estimate of the cover of short crowned trees, but would underestimate the effect of the long crowns in terms of light transmission at solar angles not directly overhead. A wide angle technique might adequately represent the long-crowned species, but might underestimate the short-crowned trees since the view of their crowns would often be covered by the deep crowned trees. With either a wide or a narrow angle technique, short trees would have greater representation than tall trees. In a mix of coniferous and deciduous trees, coniferous crown cover could be accurately measured in the autumn or spring, but deciduous cover measured in the summer would always be underestimated by the presence of coniferous trees blocking the view. Due to the distortions in actual crown cover in non-homogenous stands, wide angle techniques should be used to estimate the crown cover specific to the radiation environment of a particular spot, or many measurements must be taken to characterize the crown cover of an average spot in the understory.

Leaf Area Index

A more accurate estimation of tree crown cover would be obtained by leaf area index. Leaf area index (LAI) is the area of leaves per unit ground area

(Barbour *et al.* 1980). It is different from leaf area or percent cover in that the layering of leaves is accounted for. LAI is not measurable directly, but may be estimated by the following techniques:

Litterfall

Measuring litterfall is a fairly direct, yet tedious method of measuring LAI. Leaves are collected in traps during leaf abscission in the autumn. LAI is determined by measuring the area of the leaves per ground area. The design of traps may influence the collection of leaves resulting in over or underestimates. The method becomes complicated with conifers which retain their needles for variable numbers of years, and which may shed more needles in dry years (Pierce and Running 1988).

Sapwood Area

Since a tree can only support as much foliage as it can supply water to, sapwood area may be measured to estimate LAI or foliage biomass (Kaufmann and Troendle 1981). Correlations linking foliage biomass or LAI to sapwood area have been shown to be highly significant (Grier and Waring 1974), and more accurate than regressions using dbh for some tree species (Snell and Brown 1978). The amount of crown biomass held per area of sapwood is species specific (Oliver and Larson 1990). Sapwood area to leaf area ratios have also been shown to change with geographic location and stand density (Hungerford 1987). The tedious and costly nature of obtaining sapwood ratios, and the limited area of application, has limited this technique's use in many regions (Pierce and Running 1988). Relationships between sapwood area and LAI have not been derived for white spruce or aspen in the boreal forest or elsewhere.

Sunfleck Inversion

Sunflecks are patches of direct beam light that reach the ground through gaps in the canopy (Chazdon and Pearcy 1991). The sunfleck area below a canopy is inversely proportional to the canopy's LAI, as described below (Anonymous 1989):

sunfleck fraction (ϕ) = $e^{(-K \cdot LAI)}$

ϕ = zenith angle
K = extinction coefficient

The extinction coefficient K, is a measure of the effectiveness of a particular LAI to attenuate light. Specifically, it is a function of solar angle and leaf orientation (Monteith and Unsworth 1990). Determining the leaf angle distribution in crowns and canopies is difficult. Consequently, the value of K is often assumed or derived empirically (Jarvis and Leverenz 1983). For conifers, K has been estimated to range from 0.4 to 0.65 (Jarvis and Leverenz 1983). Pierce and Running (1988) obtained reasonable LAI estimates assuming a mid range K value of 0.52 for all coniferous stands, whereas Vose and Swank (1990) found a 0.52 value of K to cause overestimation of LAI in their eastern white pine (*Pinus strobus* L.) stands. Smith *et al.* (1991) suggest that K is too variable between stands of different stand structure and canopy architecture to use universal species averages. Black *et al.* (1991) show conclusively that extinction coefficients for Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) are solar angle dependent, and that the use of a single coefficient for different solar angles introduces considerable error. Kuroiwa (1970) added further uncertainty to the use of K values by finding that leaf angle distribution had little effect on light interception but had a large effect on light distribution within and beneath the canopy.

K values have been measured only in pure stands. As described earlier, white spruce in mixedwood stands have longer crowns than in pure stands, increasing their light attenuating capacity. Use of K values derived from pure stands in mixedwood stands might cause considerable error.

An instrument that measures sunfleck fractions is the Sunfleck Ceptometer made by Decagon Devices Inc. It is a hand-held instrument with 40 or 80 individual sensors that measure and average PAR (photosynthetically active radiation) instantaneously (line quantum sensor). To compute sunfleck fraction, a threshold level of light is selected, then the fraction of sensors reading above that amount is computed. Sunflecks below tall canopies, like those of mature trees, are affected by pronounced penumbra (partial shading around complete shadows). Penumbral effects make this method unsuitable for forest stands (Welles 1990, Anonymous 1989, Lieffers and Stadt personal experience).

Another method used to measure sunfleck fraction to obtain LAI is hemispherical photography. The temporal sampling of this method is improved from that of the line quantum sensor's instantaneous light measurements, since sunflecks may be estimated for a particular location and any number of solar angles representing different times of day or seasons (Chen *et al.* 1991). However, the line quantum sensor covers an area more efficiently spatially than hemispherical photography could since many measurements can be made rapidly. Solar angle is controlled in the photographic method, but the measurement or assumption of leaf angle distribution for the canopy is still a limitation. Further limitations of canopy photographs are discussed in the section on seasonality of light transmission.

Transmission Inversion

A better method for determining LAI in forest stands may be found in meauring canopy light transmission. This method, also possible with the Sunfleck Ceptometer or any other line quantum sensor, is based on the ratio of above to below canopy light. Many different formulas for calculating LAI from canopy transmission data have been described (Nel and Wessman 1993). This seems to indicate the variable success of any particular method. Pierce and Running (1988) used a simple formula based on Beer's Law to find the LAI of coniferous forest stands in Montana. The formula assumes that leaves in the canopy are found at any angle (spherical leaf angle distribution), and that leaves are randomly distributed throughout the canopy.

$$LAI = \frac{-\ln (Q_i / Q_o)}{K}$$

Q_i = PAR below the canopy
Q_o = PAR above the canopy
K = extinction coefficient

Above canopy PAR readings may be taken in an open area at any height, with the line quantum sensor immediately before, during, or after sampling below the canopy; if skies are uniformly sunny and sampling is done over a short time. If greater accuracy is desired, single sensors may also be used to record outside light conditions continuously while sampling.

Agreement on the estimation accuracy of transmission inversion to find LAI is lacking. Improved accuracy is attempted by adding more factors such as: specific leaf angle; zenith angle; absorption of PAR by leaves; fraction of direct to diffuse PAR; and foliage and crown distribution. Each added factor greatly increases the body of empirical data necessary to support the model, thereby increasing effort, cost and decreasing practical application.

LAI-2000

Another instrument, the Plant Canopy Analyzer, also calculates LAI from a ratio of above to below canopy light (transmission inversion), however, it is used only in diffuse light. Diffuse light is recorded from 5 sensor bands covering a hemispherical view. Sampling is restricted to overcast days but, because only diffuse light is measured penumbral effects are avoided, and more solar angles are sampled improving the estimation of the radiation environment for a particular spot. As with a line quantum sensor, many readings may be taken in rapid succession, allowing a greater area to be sampled. In effect, the LAI-2000 attempts to combine the good temporal features of the hemispherical photographs with the good spatial sampling features of a line quantum sensor. As with the line quantum sensor, the ability to sample above canopy light simultaneously, or immediately before and after below canopy sampling, is essential.

Understory Composition and Cover

Light is a limiting factor in the growth of understory vegetation including white spruce seedlings. However, the herb and shrub canopies themselves also attenuate light. Each species differs in seasonal development and morphology and therefore in the amount and nature of shade cast (DeLong 1991). Generally, plants show the greatest LAI in the spring (Uemura 1994, DeLong 1991, Hutchison and Matt 1977), with seasonal variation in the amount of LAI held related to leaf habit (Uemura 1994). Biennials and perennials showed a lower LAI maintained for most of the summer compared to annuals that showed a distinct short peak of LAI in the spring (Uemura 1994). The highest LAI held in the spring is often simultaneous with the greatest light intensities reaching the understory (Uemura 1994, Hutchison and Matt 1977). The vigour of each species, or amount of foliage held, varies not only with season, but also with the

amount of light available (Rowe 1956). Leaf habit and vigour are factors in determining how much light is attenuated by the understory at what time of year. Early successional plant species such as *Calamagrostis canadensis* (Eis 1981) and *Epilobium angustifolium* (Myerscough 1980), are able to increase their cover rapidly when high light becomes available in the understory.

The cover, LAI and structure of the understory determines how much light the understory attenuates and how much light it transmits to the forest floor. The understory is therefore another factor in judging a stand's ability to support coniferous regeneration based on light availability. Measuring understory cover is commonly done by estimating each species' percent cover individually in 1 m^2 plots. A percentage for each species is then averaged and used to estimate its cover for the whole stand. Plots often contain more than 100 % cover in total because each species is measured on an individual horizontal projection rather than all species together.

For similar reasons as noted in the previous discussion of the overstory, LAI or a measure of biomass would perhaps provide a better tool for judging the ability of the understory to attenuate light. LAI or biomass estimates may be obtained by harvesting and measuring the vegetation directly. The gap fraction and canopy transmission techniques have been used to determine LAI in agricultural crops, but have not been tested in forest understories. The large variability in composition and distribution of a forest understory canopy would seem to limit the ability of these techniques to isolate effects of individual species.

DeLong (1991) and Comeau *et al.* (1993) describe competition indices for conifer seedlings in clearcuts. Their indices were empirically derived from the available light at the top of seedlings, and the distance and height of the nearest

competitors. These indices indirectly estimate the amount of light attenuated by competing understory vegetation. The method seems useful in making vegetation management decisions on clearcuts, but cannot be implemented under an overstory canopy.

Seasonality of Light Transmission

The atmosphere and clouds scatter (reflect or transmit) direct beam radiation relative to their thickness and the solar angle (Campbell 1986). Scattered radiation (diffuse radiation) is found in all directions and is therefore less concentrated. The amount of diffuse radiation peaks at about 50 % cloudiness (Monteith and Unsworth 1990). Diffuse radiation should have better potential to reach the understory than direct beam radiation, because it penetrates from all sides (Holmes 1981). Indeed, Reifsnyder *et al.* (1971) found a uniform distribution of diffuse radiation and an irregular distribution of direct beam radiation under pine and hardwood canopies. The amount of diffuse light is far greater within the stand than outside it (Black *et al.* 1991). Although diffuse light may reach deeply into the understory, its intensity is generally very low. It is not known whether the light intensity of diffuse light reaching the forest floor is sufficient to induce photosynthesis or sustain growth.

A vital factor in any discussion of light attenuation is the ever shifting angle of solar radiation. The position of the sun in the sky is referred to as the solar angle and is measured from the horizon (elevation angle), or from the perpendicular to the horizon (zenith angle) (Campbell 1986). The sun follows a predictable daily path rising in the sky until solar noon and falling thereafter. Seasonally, this daily arc alters substantially. At the highest elevation angles the sun's rays travel the least distance through the earth's atmosphere and light intensity is highest (Holmes 1981). Light intensity is defined as the amount of

photons, or discrete bundles of energy, impacting an area per unit time, commonly expressed as Watts $m^{-2}s^{-1}$ or in ecology, as photosynthetically active radiation (PAR; 400 - 700 µm) in µmol $m^{-2}s^{-1}$ (Campbell 1986). The highest elevation angles, and the greatest light intensities occur at solar noon diurnally, and in midsummer seasonally (Sellers 1965).

Similarily, the peak in light intensity occurs over solar noon in the overstory, understory, and on the forest floor (Hutchison and Matt 1977). Not only does solar radiation pass through more atmosphere at lower elevation angles, it also travels a greater distance through a forest stand. The longer path means that the probability of light being absorbed or reflected by leaves, branches, and boles before reaching the ground is greater. Viewed another way, shadows become longer at lower elevation angles.

While the light intensity pattern of the understory is similar to that of the overstory diurnally, the seasonal pattern is not. Seasonal changes in the overstory canopy, not only solar angle, control the amount of light reaching the understory (Hutchison and Matt 1977). A greater percentage of light is expected to reach the understory and forest floor in the spring before aspen trees and the understory become fully leafed, and in the autumn when overstory aspen and the understory shed their leaves. The intensity of light in the spring and particularily in the autumn, however, is reduced from that of midsummer by a lower solar angle.

In the mixedwoods of Alberta, aspen leafing does not begin until approximately mid May, when the solar elevation is already quite high. Understory growth below deciduous canopies would receive relatively high doses of light at this time (Hutchison and Matt 1977). Ross *et al.* (1986) surveyed PAR below coniferous and mixedwood overstories in the boreal forest of

Alberta. They found significantly higher amounts of PAR below mixedwood overstories in the spring (May), but not the autumn (September). Pure coniferous overstories showed no significant difference in light transmission throughout the summer, unless there was a tall (> 1 m) deciduous understory present. Uemura (1994) measured light transmission through deciduous, coniferous and mixed stands in Japan. All stands showed highest light transmission in the spring with a dramatic decrease to low levels of light transmission in the summer. The mixedwood and oak (*Quercus mongolica*) - maple (*Acer mono*) stands showed a second peak in light transmission in the autumn, while the coniferous (*Picea jezoensis* and *Abies sachalinensis*) and beech (*Fagus crenata*) stands showed similar or decreased light transmission in the autumn compared to summer levels. The spring leafless period may be an important period in the growth and survival of white spruce seedlings below aspen or mixedwood canopies if other factors are not limiting. It has not been investigated whether a similar seasonal pattern of light availability exists beneath the understory canopy on the forest floor.

Hemispherical Photography

A method that traces the effect of solar angle on canopy light attenuation and light penetration to the understory is hemispherical photography. Different solar paths may be traced on the photograph and radiation summed for the day, week or season. An obvious limitation is that several photographs need to be taken in deciduous or mixedwood stands to adequately represent the change in foliation over the growing season.

An important source of error may occur in capturing the image on film. High contrast film is used to make foliar outlines clear. Depending on the exposure and focus used, this may increase or decrease the image of the leaf on film (Chen *et al.* 1991). Chen *et al.* (1991) found it necessary to underexpose

images from the camera's recommended aperture, by 4 - 5 stops on sunny days, and 1 - 2 stops on overcast days to achieve accurate LAI readings. Aspen crowns transmit much more light than white spruce crowns. It is not clear whether the canopy photograph method can adequately record and quantify porous or translucent canopies such as those of aspen. A mix of translucent and opaque canopies, like those of aspen and white spruce, would further complicate the analysis. Also, it would not be possible to distinguish between tree species on the preferred high contrast black and white film. Distinction between aspen and white spruce might be possible manually on color photographs, but would be error prone and tedious. The large aperture of a fisheye lens is able to achieve focus of both the very near and very far foliage, however, it is unlikely that different vegetation layers could be distinguished in the analysis.

Predicting Light Transmission Through Mixedwood Stands

The Theoretical (Modelling) Approach

Methods of estimating light attenuation with a theoretical approach are numerous and vary in detail and complexity. In the simplest models, light is measured above and below the overstory canopy, leaf angle distributions and extinction coefficients are measured or assumed, and a form of Beer's Law is implemented.

It has been shown that some pure forest canopies do not exhibit exponential light extinction (Beer's Law). Vose and Swank (1990) found a linear relationship between PAR transmittance and LAI in a 32-year-old eastern white pine stand, and Reifsnyder *et al.* (1971) found an exponential relationship for a 36-year-old red pine (*Pinus resinosa* Ait.) stand, but a linear relationship for a 70-year-old hardwood stand. These discrepancies are likely the result of violations

of the homogeneous canopy assumption of Beer's Law (Vose and Swank 1990, Reifsnyder *et al.* 1971).

Mixedwood stands violate the homogeneous canopy assumption of Beer's Law, however, Cannell and Grace (1993) describe how Beer's Law may be expanded to predict light transmission through a stand made of two separate homogeneous canopies:

$$T = I_a e^{-K_1L_1 - K_2L_2}$$

T = Light transmission (PAR)
I_a = PAR above the canopy
K_1 = extinction coefficient tree species 1
L_1 = leaf area index tree species 1

The formula may work well, but finding the LAI and K values of even one of the species remains difficult. As discussed earlier, LAI and K values from pure stands are not applicable to mixed stands. This formula assumes a random distribution of each of the overstory foliage types. Cannell and Grace (1993) point out that this is a poor approximation, especially for coniferous canopies. Coniferous canopies are thought to show more clumped than random distribution of leaves resulting in greater transmittance (Black *et al.* 1991, Nilson 1971). Some more advanced models can account for distinct grouping or clumping of trees (Black *et al.* 1991, Norman and Jarvis 1975) and crowns (Norman and Welles 1983, Kuuluvainen and Pukkala 1989). These models require considerably more information about the canopy than a random model would. Further, most boreal mixedwood forests likely show clumped tree species distribution. The clumping of tree species has not been not yet been considered in modelling light interception or transmission in mixed stands,

although the arrangement of tree density (clumping) has been considered in monocultures (Oker-Blom *et al.* 1991, Norman and Jarvis 1975).

Cannell and Grace (1993) also propose a model of light penetration through an over-and understory, as the subtraction of light lost to each canopy layer above from full light:

$$T = I_a e^{-\kappa_o L_o - \kappa_u L_u}$$

K_o, L_o = overstory K, LAI
K_u, L_u = understory K, LAI

Measuring the LAI of the understory may be simpler (although not less tedious), but little is known about K values or the leaf angle distribution of the many species found in the understory. Further, due to the many species in the understory canopy, the possible species composition combinations are practically infinite. Strictly applied, the homogeneous canopy assumption of Beer's Law could never be met. Perhaps grouping of understory species with similar K values could produce a manageable model.

The Empirical Approach

The goal of empirical methods is to find a simple measure that has some quantifiable relationship to the amount of light attenuated by an overstory canopy and the amount of light reaching the forest floor. Such a relationship would yield information useful to managers wishing to regenerate shelterwood or partially cut stands. Simple stand measures such as dbh, basal area, crown closure and stand density have generally not provided good estimates of LAI or light attenuation; although they have been useful in specific cases. Jenkins and Chambers (1989) found percent crown cover measured with a densiometer and percent of basal area removed (when initial stands had crown closure) showed a

strong linear relationship with light reaching the understory in mature hardwood stands. However, dbh, initial basal area, tree height, height to the live crown, and crown depth did not yield a dependable relationship with light reaching the understory. It is not clear at what height their light measurements were made, however, since they removed all woody vegetation 10 cm or smaller, the effect of an understory canopy on forest floor light was not considered.

In mixedwood stands, the standard mensurational measurements seem very poor descriptors of the light intercepting ability of the radically different white spruce and aspen crowns. Lieffers and Stadt (1994) found that understory light (at 1.3 m) increased with increasing basal area of aspen in mixedwood stands and decreased with increasing basal area in white spruce dominated stands. Understory light (at 1.3 m) was also found to increase with age of aspen dominated stands. Increased basal area in these stands is more likely an indication of increased age (larger diameter trees) than of densely stocked stands. With increased age (past maturity) aspen crowns tend to show decreased LAI , and individual trees die or are windthrown from internal rots (Peterson and Peterson 1992) leading to increased light transmission. Since it is the difference in crowns of aspen and white spruce that causes the difference in their light transmission, simple measurements that quantify their crowns might prove more useful in mixedwood stands.

Crown cover could be estimated with a densiometer if it were possible to distinguish between tree species. However, the results may not accurately account for crown density or opaqueness. This problem has not been studied. Canham *et al.* (1994) used the hemispherical photograph approach to compare the shading capacity of deciduous tree species over a broad range of solar angles in New England. Stand level light transmission was not evaluated, likely due to the relatively small number of sampling points possible with this method.

Crown areas could be estimated from height, width and taper, and combined with an estimation of crown light transmission or opaqueness to quantify how much light is intercepted. Average vertical crown area per species could then be combined with stand densities and solar angles to estimate the amount and nature of shade cast for the stand. It would be difficult to project tree level light transmission to stand level light transmission, due to the increased overlapping of shadows from different crowns with solar angle. Light transmission and crown shading has not been studied on individual trees, although there have been many studies on stand level light transmission through various pure overstory canopies.

Many instantaneous measures are required to obtain stand level light information because of the large variation in light spatially and temporally (Anderson 1970). Pierce and Running (1988) tested the effect of the number of spot measurements taken (sample size) with a line quantum sensor with estimation error of LAI. The relationship they found shows a substantial decrease in error up to a sample size of 30. Little more accuracy was gained with more than 30 sampling points. It should be noted that an individual light sample covered approximately. 9 m^2 and was an average of 20 measurements.

In order to make light measurements taken on one day comparable to those taken on another, the percent rather than the actual value of light penetrating the canopy should be measured. Further, by limiting the change in zenith angle, variation in light penetration due to length of the solar path through the canopy is reduced. This restricts light measurements to a few hours over solar noon, and to days within the same season. It is possible to correct light intensity measurements made on a horizontal plane, for changes in solar angle by a cosine angle correction. However, changes in light intensity due to different path lengths through the overstory canopy with changing solar angle

are more difficult to correct, since K (the transmission extinction coefficient of a crown), is dependent on solar angle.

An underlying problem in all empirical studies seems to be the lack, or uncertainty, of applying the results to other species, areas, and silvicultural systems.

The purpose of the following studies was to: quantify light penetration to the forest floor of boreal mixedwood stands as affected by over- and understory canopies in the spring, summer and autumn; and, to quantify differences in light transmission through individual aspen and white spruce crowns. The objective is to supply information on the light available for white spruce advance regeneration and its competitors in the understory of mixedwood stands.

Based upon this literature review, we decided to use a quantum line sensor (Sunfleck Ceptometer, model SF-80, Decagon Devices, Inc., Pullman, WA) to measure light transmission through canopies/crowns in two studies (Chapter II and III). Due to the speed of measurement possible with the Ceptometer, many measurements could be made covering a large area within a narrow range of solar elevation angle change.

Methods of measuring overstory (spherical densiometer) and understory (1 x 1 m percent cover plots) canopy cover were attempted. In general, the inaccuracies and flaws in application of the methods between the different seasons negated their use in analysis with light transmission measurements. With the spherical densiometer, crown cover of white spruce could be adequately estimated in the spring and autumn when the aspen were leafless. The aspen component of the overstory however, was underestimated in the summer due to the long crowns of white spruce that blocked the view of the observer. Changes in understory cover between the seasons were not

adequately quantified with the percent cover plots. Understory species were tallied individually resulting in skewed total cover estimates, especially between seasons.

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Chapter II.

Seasonal Patterns of Light Transmission Through Boreal Mixedwood Canopies

Introduction

Managers often have difficulty in achieving sufficient white spruce (*Picea glauca* (Moench) Voss) regeneration on clearcut sites in the boreal mixedwoods (Weetman 1989, Drew 1988, Henderson 1988). As a result there is great interest in silvicultural systems that protect and promote white spruce advance regeneration (Navratil *et al.* 1994, Youngblood 1990, Brace and Bella 1988, Froning 1980). While advance regeneration may occur naturally without stand manipulation, stocking is frequently inadequate or unpredictable (Weetman 1989). Apart from seed sources, it is not clear why some stands achieve much more advance regeneration than others. Information is needed on the stand characteristics that create an environment conducive to advance regeneration. One of the greatest difficulties in regenerating white spruce in the boreal mixedwoods is competing vegetation (Weetman 1989, Drew 1988, Eis 1981). Lieffers and Stadt (1994) investigated the effect of overstory basal area and stand age on competing vegetation cover and white spruce sapling growth. They found aspen-dominated stands transmitted between 15 - 40 % light to a height of 1.3 m; this limited competing vegetation while allowing for acceptable white spruce sapling growth. Other studies have investigated the growth of white spruce at different percentages of light transmission (Brix 1972, Logan 1969, Eis 1967). On the forest floor level, however, the amount or percent of light transmission available to seedlings is not known. A stand that transmits sufficient light through the overstory, may not transmit enough light through the understory to sustain white spruce seedlings.

The strategy of evergreens in the understory is to achieve part of the annual carbon fixation during the leaf-off periods of over-and understory deciduous species (Young 1985, Lassoie *et al.* 1983, Chabot and Hicks 1982). In general, in deciduous stands of *Liriodendron tulipifera* (Hutchison and Matt 1977); *Populus tremuloides* (Ross *et al.* 1986); *Fagus crenata, Quercus mongolica* and *Acer mono*, and coniferous stands of *Picea jezoensis* and *Abies sachalinensis* (Uemura 1994), *Pinus elliottii* (Gholz *et al.* 1991, Dalla-Tea and Jokela 1991), *Pinus strobus* L. (Vose and Swank 1990) and *Pinus taeda* (Dalla-Tea and Jokela 1991), there was more light transmitted through the overstory to the understory in the spring than in the summer. Although theoretical models have been proposed (Cannell and Grace 1993), it is not clear what the effect of stand age (Brown and Parker 1994, Lieffers and Stadt 1994), mixed compositions (deciduous-coniferous) and understory vegetation have on light transmission to positions above shrub and herb layers or at ground levels where seedlings must establish.

The objective of this study was to quantify light penetration to the forest floor of hardwood and mixedwood stands as affected by over- and understory canopies in the spring, summer and autumn. Based on light penetration, the ability of the stands to support white spruce advance regeneration is discussed.

Study Sites

Six stands were chosen in each of three age/forest compositions of a boreal mixedwood ecosystem near Whitecourt, Alberta (54° 10 ' N, 115° 40' W). The Boreal Mixedwood Region is a common forest association throughout the boreal forest region of Canada (Rowe 1972). Three overstory forest types were chosen: pure, young (10 - 20 years old) aspen stands; pure old (more than 80 years old) aspen stands, and old mixed white spruce - aspen stands. These are overstory types in which white spruce regeneration is desireable. Common

shrubs associated with white spruce and aspen in these stands were: *Rosa acicularis* L.; *Lonicera involucrata* (Richards.) Banks; *Amelanchier alnifolia* Nutt. and *Sheperdia canadensis* (L.) Nutt. Dominant herbs and grasses were: *Viburnum edule* (Michx.) Raf.; *Epilobium angustifolium* L.; *Aralia nudicaulis* L. and *Calamagrostis canadensis* (Michx.) Beauv. Stand composition resembled the Lower Boreal Cordilleran (LBC) 5 association (Corns and Annas 1986). Criteria for selecting stands were overstory composition, age, a size large enough to contain a 30 x 30 m plot with 20 m buffers, reasonably uniform stocking of overstory trees, good health, less than 5 % slope, a nearby open area for recording full light, and less than 20 % shrubs or saplings taller than 1.3 m. The shrub criteria eliminated those stands with a heavy growth of *Alnus crispa* Michx.

Materials and Methods

One 30 x 30 m plot with 20 m buffers was placed randomly in each of the 18 stands. Basal area of overstory trees was estimated in five spots, at plot centre and at 6 m from the plot corners towards plot centre, with a 4 BAF prism for old stands and with a 2 BAF prism for young stands (Table II-1). Stand age was estimated from tree ring counts taken from the three largest trees of each species in a stand (Table II-1).

Light transmission was measured with a hand-held integrating radiometer (Sunfleck Ceptometer, model SF-80, Decagon Devices, Inc., Pullman, WA). The 80 cm long probe measures photosynthetically active radiation (PAR; 400 -700 µm) simultaneously with 80 sensors. The radiometer's microprocessor averages and stores any number of readings taken with the time of day. Inside the stand, measurements were taken at three height levels: at 1.3 m (below the overstory); at 0.5 m (below the shrub layer) and on the forest floor at 0 - 0.05 m (below the herb layer). Thirty points in a systematic 5 x 6 m grid were sampled

in each plot. At each grid point, 12 PAR readings were taken with the radiometer in a circle, holding it at an arm's length at each height level. The effective sample area of each height level was approximately 7 m^2 and contained 960 individual readings. Care was taken to hold the radiometer level and not to shade the probe or trample vegetation while measuring. In an adjacent open site, a single PAR sensor (Quantum Sensor, LI-190SA, LI-COR Inc., Lincoln, NB) and a datalogger (CR21, Campbell Scientific Co., Ltd., Logan UT) recorded PAR at one minute intervals. At the start and end of sampling each stand, light readings from the radiometer were compared to the single sensor in order to standardize their readings.

PAR measurements were made on sunny days only, from 10:00 to 14:00 solar time, at three times throughout the growing season: in the summer of 1993, with full leafing of aspen (June 10 - July 30); in the autumn of 1993 with at least 80 % aspen leaf-off (only 3 stands of each overstory type were sampled) (Oct. 7 - Oct. 10) and in the spring of 1994, with less than 20 % bud burst (April 28 - May 8). All 30 readings per height level were averaged to derive a stand level estimate of light transmission at that height. Percent light transmission was calculated by dividing the PAR readings below the canopy by the readings from above the canopy. By measuring total light transmission at three heights, the amount and proportion of light attenuated by the herb, shrub and overstory canopies could be found individually. The percent light transmission of each canopy layer individually was calculated as: percent light received below the canopy layer / the percent light available above the canopy layer. PAR measurements presented as absolute values were corrected by a sine transformation based on the incident solar angle. This corrected for holding the radiometer parallel to the ground rather than perpendicular to the changing incident solar beam. The angle of the solar beam was calculated from the location, day and time of measurement of each stand. This correction should

allow an estimate of the light for photosynthesis on foliage with random leaf orientation.

Stand level averages of light transmission were used to compare seasons, overstory types and height levels in a split plot design (Appendix I). Tests of sphericity showed that the seasonal data was not acting as a repeated measure (Huynh-Feldt Epsilon = 0.78) and that a split plot design could be used (Ott 1993). One-way analysis of variance (ANOVA) and contrasts were used to further describe significant differences between light transmission means. All statistical analyses were conducted using SAS version 6 (SAS Institute Inc., Cary, NC).

Results

Although light intensity was highest in the summer, light transmission to the forest floor was equally low in all forest types (Fig. II-1b; $p > 0.05$, Appendix I-b). Only 6 - 7 % of incident light (approximately 98 - 118 $\mu mol\ m^{-2}s^{-1}$) was received, despite large differences in the amount of light transmitted through the over- and understories of the mixed and pure aspen stands. The overstory of the old aspen stands transmitted more light (32 %) to the understory than the young aspen (19 %) or mixed stands (14 %) (Fig. II-a). Consequently, the understory of the old aspen stands transmitted much less light (19 %) to the forest floor than the young aspen (33 %) or mixed stands (50 %) (Fig. II-2b). Essentially, the more light that passed through the overstory canopy, the more light was attenuated by the understory vegetation.

In the autumn, lower solar elevation angles (approximately 30° from the horizon compared to 50° in the spring and 60° in the summer) increased the length of the path of light through the canopy, resulting in tree boles and crowns intercepting more light. More light was transmitted to the forest floor in the

pure aspen stands because of the loss of deciduous cover in the overstory (Fig. II-1c). Although the deciduous understory vegetation was dead, much of the leaf litter was still held in place. Combined with low solar elevation angles, the herb and shrub layers still attenuated a proportion of incoming radiation (Fig. II-2b). Despite the lower solar angles which caused lower light intensities above the canopy, ground level light was approximately 320 $\mu mol\ m^{-2}s^{-1}$ in the old aspen stands, and 470 $\mu mol\ m^{-2}s^{-1}$ (Fig. II-3) in the young aspen stands in the autumn months. In the mixed stands, no more light was transmitted through the overstory to the forest floor (8 %) than in the summer, despite the loss of deciduous cover. Coupled with decreased above canopy light intensities, much less light was actually available on the forest floor (62 $\mu mol\ m^{-2}s^{-1}$) than in the summer (Fig. II-3).

The deciduous leaf-off period in the spring, with relatively high solar elevation angles, showed the most light penetrating to all understory levels in all overstory types (Fig. II-1a). The pattern of light penetration and attenuation was similar to that of the autumn period. However, less light interception due to shedding or flattening of dead understory vegetation over the winter, and higher solar angles resulted in overall increases in percent light transmission. On the forest floor, the highest light intensities were found in the young (43 % or 790 $\mu mol\ m^{-2}s^{-1}$) and old (40 % or 730 $\mu mol\ m^{-2}s^{-1}$) pure aspen stands. Even in the mixed stands, 18 % light was transmitted to the forest floor (310 $\mu mol\ m^{-2}s^{-1}$).

Based upon corrected PAR values, the least light occurred on the forest floor in the mixed stands in the autumn (62 $\mu mol\ m^{-2}s^{-1}$); slightly more was available in all stands in the summer (approximately 110 $\mu mol\ m^{-2}s^{-1}$); and in the spring 310 $\mu mol\ m^{-2}s^{-1}$ was available in the mixed stands, and 760 $\mu mol\ m^{-2}s^{-1}$ in the pure aspen stands (Fig. II-3). A wide range in light intensities were transmitted through the pure aspen overstories to 1.3 m over the three seasons; in the young aspen stands from 328 $\mu mol\ m^{-2}s^{-1}$ in the summer to

1115 µmol $m^{-2}s^{-1}$ in the spring (Fig. II-3). Light transmission through the overstory to 1.3 m changed less between seasons in the mixed stands. Transmission decreased from spring values of 383 µmol $m^{-2}s^{-1}$ to 251 µmol $m^{-2}s^{-1}$ in summer, and autumn values of 97 µmol $m^{-2}s^{-1}$.

In the summer, mixed overstories transmitted an average of 14 % PAR, while the young aspen overstories transmitted 19 % and the old aspen overstories 32 % (Fig. II-2). The understory of the mixed stands transmitted 50 % of the light incident at that level, while the young aspen understories transmitted 33 %, and the old aspen understories transmitted 19 %. Substantially more light was attenuated by the understory of old aspen stands than the overstory. In general, the light attenuation of individual canopy layers was highest in the fully-leafed summer, and lowest in the spring before leafing, except for the overstory of mixed stands (Fig. II-2); in these stands, autumn light attenuation was similar to that of the summer.

Discussion

The amount of light transmitted to the forest floor was very low (6 - 7 %) under all overstory types in the summer (Fig. II-1b). The increased overstory light transmission in the aspen stands leads to increased development of the understory layers. As early as 1956, Rowe described the shift in understory cover from tall shrubs and tall herbs in pure *Populus* stands, to low herbs and mosses in pure white spruce stands, driven by decreasing light transmission through increasingly coniferous dominated overstory compositions in the boreal mixedwoods. Recently, Cannell and Grace (1993) advanced a similar theoretical model of increasing understory leaf area index (LAI, leaf area per unit ground area) with decreasing overstory LAI. Our data support this relationship, as seen in the summer, of reduced leaf area in the overstory transferring to the

understory (Fig. II-2). The mixed stands had the greatest PAR interception in the overstory, the least in the understory. The young and old aspen stands had the least PAR interception in the overstory and the most in the understory. The net effect of this variable distribution of LAI between the over- and understories in the summer is equal light transmission to the forest floor regardless of overstory composition or LAI.

In general, substantially more light was transmitted to the forest floor in the deciduous leaf-off periods in the spring and autumn than in the fully leafed summer. The effect was most pronounced in the pure aspen stands which had a greater deciduous leaf area in the overstory (Fig. II-3). Hutchison and Matt (1977) and Uemura (1994) found a similar pattern of high light penetration to the forest floor in the spring leafless period with a sharp decline to low levels of light penetration in the summer in deciduous forests.

The 1.3 m light measurements in mixed stands recorded in this study showed a similar seasonal response to two aspen-white spruce mixed stands measured by Ross *et al.* (1986) despite differences in stand ages between the two studies. They found percent light transmission in the autumn was not significantly greater than in the summer, nor significantly less than in the spring. Ross *et al.* (1986) suggested that seasonal light transmission in the mixedwoods emulated that of deciduous dominated forests. However, we found large seasonal differences in overstory light transmission in deciduous stands. In general, deciduous stands show a period of increased light penetration in the autumn (our data Fig. II-3, Uemura 1994, Hutchison and Matt 1977), while in pure coniferous stands light penetration continues to decrease (Gholz *et al.* 1991), or shows no significant difference from summer levels (Uemura 1994, Dalla-Tea and Jokela 1991, Vose and Swank 1990). Gholz *et al.* (1991) concluded that light penetration through coniferous stands was more sensitive to the large seasonal

changes in solar angle than to seasonal changes in LAI. Since the difference in crown shading capacity between aspen and white spruce is large when deciduous trees are leafless and solar elevation angles are low, the ratio of white spruce to aspen in the overstory will likely control the amount of light transmitted through mixed stands.

The young aspen stands transmitted substantially more light than the old aspen stands in the autumn, only slightly more in the spring, and generally less in the summer (Fig. II-2). The young stands also showed greater variability in light transmission than the old stands, likely due to irregular natural restocking (the young aspen stands had approximately 13 700 stems per hectare). Differences in light transmission between the young and the old aspen stands however, are likely due to the geometry of light transmission. Higher wood shading area in old aspen stands would decrease light transmission over that of young aspen stands in the leafless autumn. In the summer, higher crown closure in young stands (Peterson and Peterson 1992) and the penumbral effects of gaps through taller and shorter overstory canopies (Smith *et al.* 1989) likely caused decreased light transmission through the young stands. In the leafless spring, wood shading area would have less effect because solar angles are much higher than in the autumn.

For white spruce seedlings in the understory of boreal mixedwood stands, season, overstory composition and seedling height are important in determining how much light is available for photosynthesis. In summer at midday, an average of 110 $\mu mol\ m^{-2}s^{-1}$ PAR was available to seedlings 0 - 0.5 m in height. Although this is above the photosynthetic compensation level of white spruce needles or shoots (K. Greenway 1994 unpublished data, Leverenz 1987), it represents only a short period of time (sunny days, at midday) in which enough

photosynthate must be produced to support the entire seedling over the much longer time span when light levels are below photosynthetic compensation.

In the mixed stands in the autumn, white spruce seedlings in the understory would receive even less light (from 62 μmol $m^{-2}s^{-1}$ on the forest floor to 97 μmol $m^{-2}s^{-1}$ at 1.3 m) than in the summer (Fig. II-3). This is likely part of the reason for poor understory development in these stands (Rowe 1956). The average light intensities found in the mixed stands in the spring (311 μmol $m^{-2}s^{-1}$ PAR) are well above compensation but also well below photosynthetic saturation levels for white spruce (600 μmol $m^{-2}s^{-1}$; Draper *et al.* 1985). Lieffers and Stadt (1994) generally did not find white spruce saplings under a range of overstory types, when light transmission to 1.3 m was less than 10 % in the summer. The mixed stands we studied transmitted an average of 12 % light to 1.3 m in the summer. Growth rates of any white spruce advance regeneration under these low annual light conditions would be very low (Brix 1972, Logan 1969). Increased height of seedlings or saplings in these stands would not result in increased growth because the shading is mostly related to overstory light interception.

If spring and autumn conditions are considered, light levels for growth of white spruce advance regeneration were much higher in the pure aspen stands than in mixed stands. Light penetration to the forest floor was well above photosynthetic compensation in the autumn deciduous leaf-off period, and above saturation levels in the spring leafless period. More light would be available to advance regeneration greater than 0.5 m in height with light intensities above the photosynthetic compensation level in the summer and above saturation levels in the autumn in the young aspen stands and in the spring in both young and old aspen stands.

The leafless period in the spring provided the greatest light intensities for light capture by white spruce seedlings in the understory of all overstory types. This period could be especially important for photosynthesis of white spruce seedlings in mixed stands, because it was the only season in which ground level light was well above the photosynthetic compensation point. The importance of this time for photosynthesis is not clear, but there is a four to six week period during and after snowmelt when there is potential for photosynthesis to occur. Preliminary work (R. Man and V. Lieffers unpublished) suggests that photosynthesis of white spruce begins a month or more before leaf-out of aspen.

The results of this study show that understory light is limiting to white spruce regeneration in the summer, and also in the autumn in mixed deciduous-coniferous stands. Silvicultural manipulation to increase light availability on the forest floor should consider the seasonal effects of overstory composition on understory cover and the importance of understory layers for summer light attenuation in deciduous stands. White spruce advance regeneration may rely on high light conditions during deciduous leaf-off in the spring, and in the autumn in deciduous stands, for survival in boreal mixedwood stands.

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Overstory Type	Stand Age		Basal Area (m^2/ha)		
	deciduous (range)	coniferous (range)	deciduous	coniferous	total (st.dev.)
Old Aspen	95 (85-138)	n/a	37.5	0.4	37.9 (4.7)
Old Mixed	105 (78-135)	92 (73-104)	27.4	21.1	48.4 (13.6)
Young Aspen	16 (10-21)	n/a	17.6	1.9	19.5 (8.1)

Table II-1. Average age, basal area and overstory composition of six stands in each of three overstory types in the boreal mixedwoods.

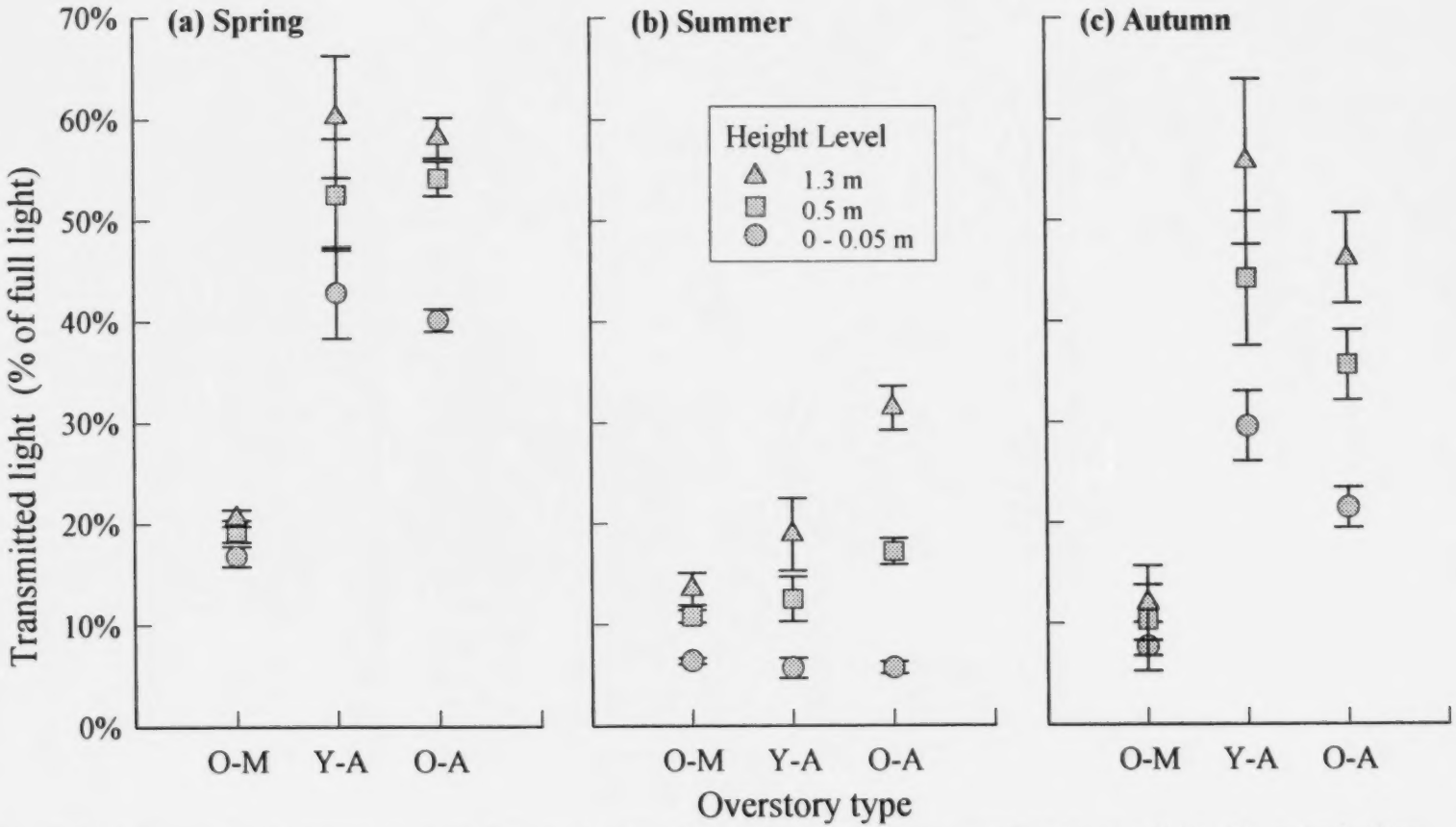

Fig. II-1. Average light transmission at three understory height levels in three overstory types: O-M, old, mixed white spruce - aspen stands; Y-A, young aspen stands; O-A, old aspen stands (means ± standard error of the mean); n = 6 (spring and summer), n = 3 (autumn).

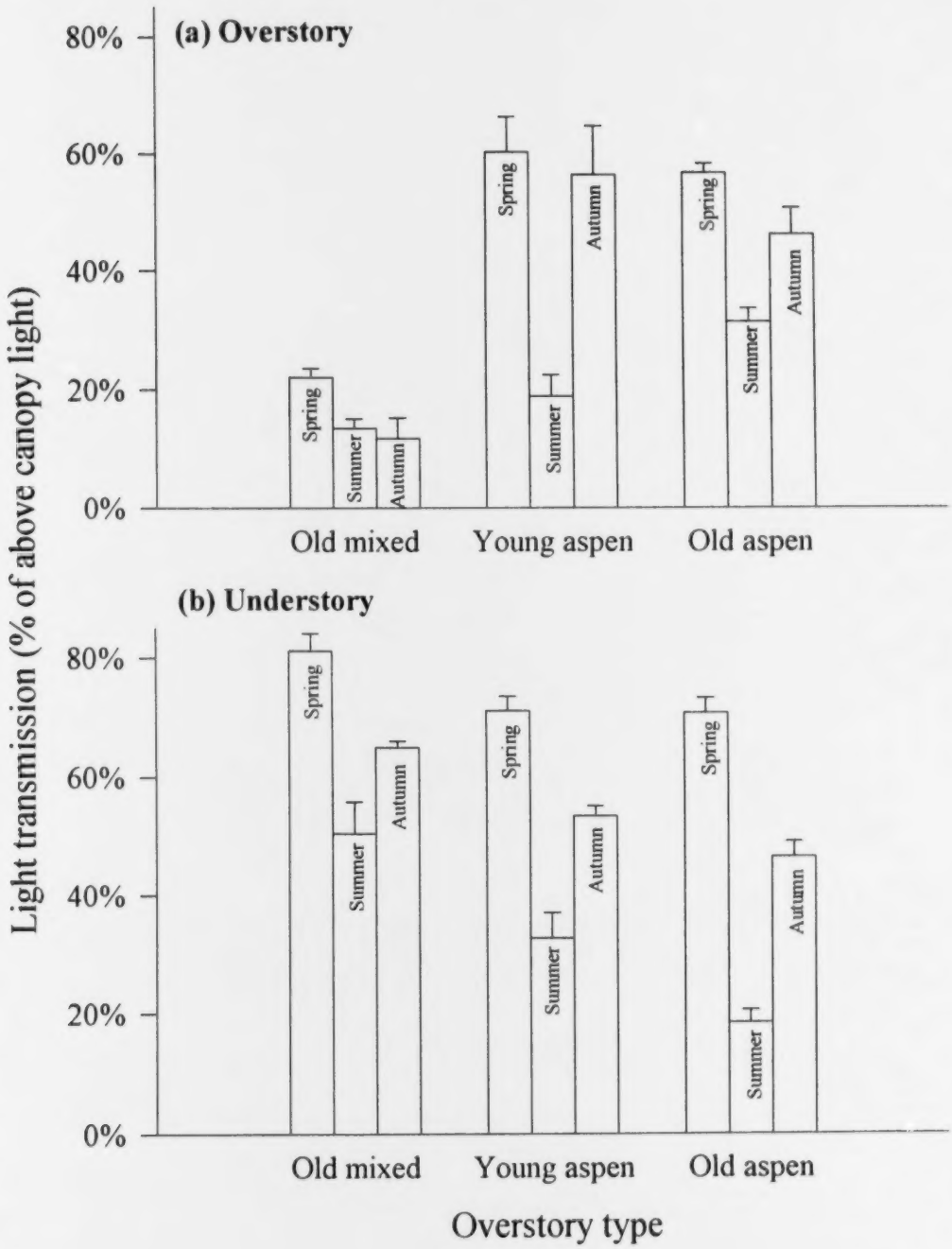

Fig. II-2. Light transmission of over- and understory canopies individually, in relation to three seasons and three overstory types. Transmission was calculated as: light below canopy / light above canopy.

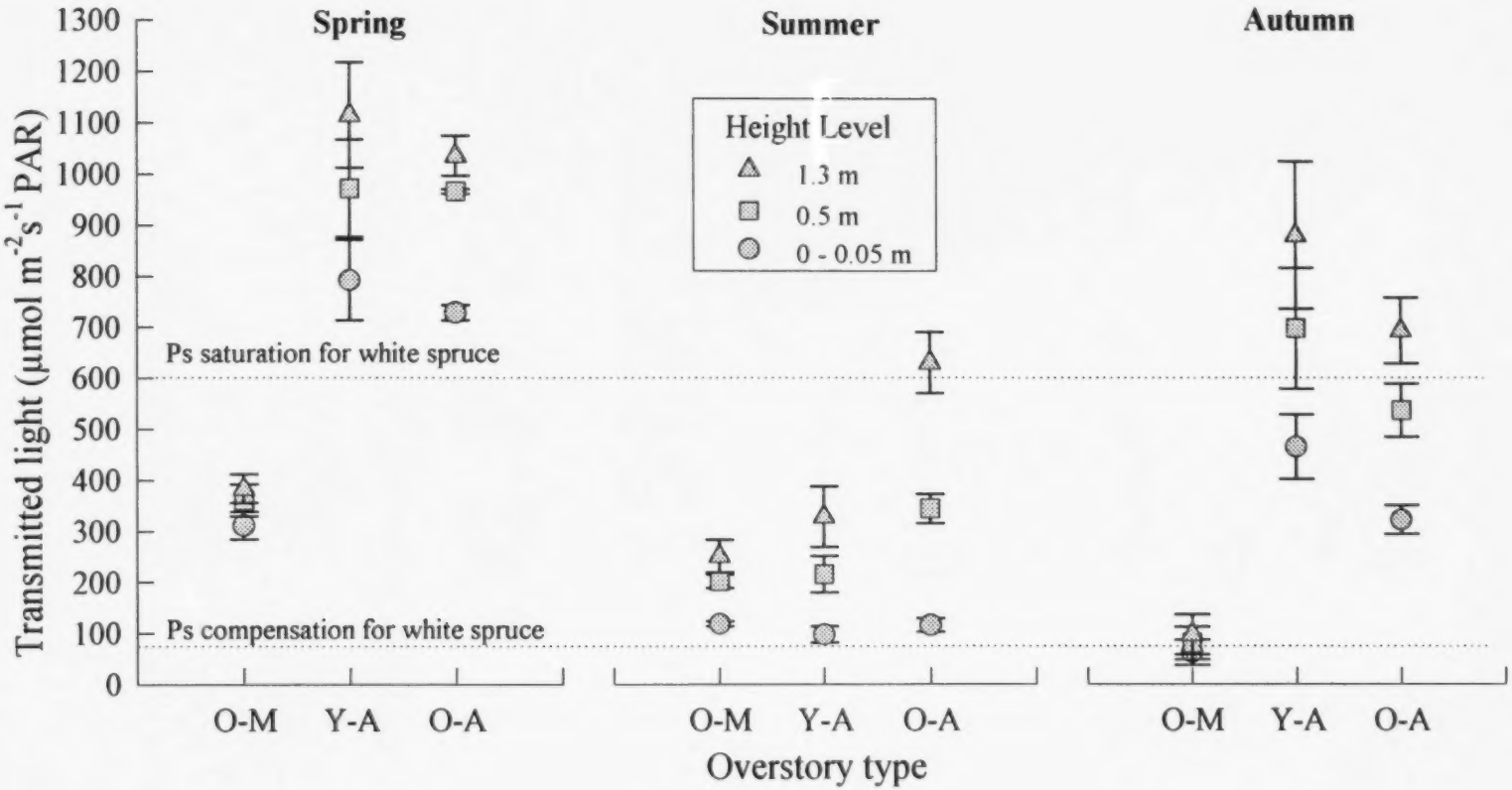

Fig. II-3. Average PAR transmission, corrected to the normal of the incident solar beam, at three understory height levels in three overstory types: O-M, old, mixed white spruce - aspen stands; Y-A, young aspen stands; O-A, old aspen stands (mean ± standard error of the mean); n = 6 (spring and summer), n = 3 (autumn).

Chapter III.

Light Transmission Through Individual Tree Crowns of *Picea glauca* and *Populus tremuloides*

Introduction

White spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.) are two common tree species of the boreal forest region of Canada (Rowe 1972). White spruce is a late successional tree species that is intermediate in tolerance to shade (Nienstadt and Zasada 1990), while aspen is an early successional tree species that is rated very intolerant of shade (Perala 1990). The existence of many different mixtures of the two tree species on the same sites, is the result of complex successional stand development driven by shade tolerance, growth rates and longevity of the species (Oliver 1981, Connell and Slatyer 1978).

Canham *et al.* (1994) found a strong relationship between shade tolerance and successional status of deciduous and coniferous tree species and the capacity of their crowns to attenuate light in a northern temperate forest. Trees with high shade tolerance did not transmit much light through their crowns, while trees with low tolerance transmitted much more light. This relationship may also apply to white spruce and aspen in boreal mixedwood stands.

White spruce trees have long, narrow crowns which may extend almost to the ground in mixed stands. White spruce crowns seem particularily well suited to capture light at low solar angles in the spring and autumn when the aspen trees have lost their leaves (Chapter II). In comparison, aspen have much shorter crowns. Aspen leaves "tremble" or flutter due to flattened petioles.

Wind may cause rapid variation in the amount of radiation passing through a canopy (Norman and Tanner 1969) and may increase light transmission through aspen crowns in the summer. Due to crown size and foliar characteristics, the shade cast by white spruce and aspen is expected to differ substantially in size and darkness. Further, crown geometry and leaf angle are expected to affect shadow size and darkness with changing solar angle. Canham *et al.* (1994) found shade tolerant species in New England to cast deeper shade due to their longer crowns, not due to a higher density of foliation. The most light was transmitted through their stands when the sun was highest in the sky.

Mixed stands of white spruce and aspen created a much darker light environment in the understory than pure aspen stands (Chapter II). White spruce, a late successional and more shade tolerant tree species, seemed responsible for the difference in the understory light environments. Lieffers and Stadt (1994) showed that, in a range of mixed stands, increases in the proportion of softwood basal area decreased light transmission, whereas increases in hardwood basal area increased light transmission. The inverse relationship between hardwoods and softwoods implies that their crowns have very different abilities for light interception. Differences in crown shape (geometry) and the shape and orientation of needles/leaves are important in determining how much light is intercepted and transmitted through individual shoots and crowns (Kellomaki *et al.* 1984). However, the effect of the individual crowns of white spruce and aspen on light transmission to the understory has not been studied.

Models for transmission or interception of light by pure stands of conifers have been proposed for *Picea sitchensis* (Norman and Jarvis 1975), *Picea engelmanni, Pinus contorta* (Oker-Blom *et al.* 1991), and *Pinus elliottii* (McKelvey 1990). A theoretical model of light penetration through mixed species stands

has been proposed by Cannell and Grace (1993) based on agricultural models. Difficulty in estimating leaf area and the extinction coefficient (K) at varying solar angles, with tree canopies of different heights, and the effect of one species on the form and light intercepting capacity of the other, preempts the use of mechanistic models of light transmission. In this chapter we take a more empirical approach to estimating effects of each species on light transmission, and estimate the change in shadow areas of white spruce and aspen over changing solar elevation. Knapp and Williamson (1984) described shadows cast by paraboloids, cones and ellipsoids at different solar elevations and slopes. With trees of the same crown length and radius, ellipsoids cast the largest shadows, and cones the least. Shadows, and the difference between the geometric shapes, were largest at lower solar elevations.

The objective of this study was to quantify the size of white spruce and aspen crowns, and to compare light transmission through their crowns over varying solar elevations. These data provide an important step in the modelling of light transmission in mixedwood stands.

Study Site

The research was conducted in an aspen-dominated mixedwood stand which had a sparse component of white spruce. The stand is located 35 km NW of Edson, Alberta (53° 40' N, 116° 40' W). The mixed white spruce-aspen stand was partially-cut in February 1994, leaving overstory white spruce, aspen and understory white spruce. Stand age was estimated to be 111 years based on ring counts from the cut white spruce.

Materials and Methods

Measurements of light transmission were taken beneath the crowns of 30 randomly chosen trees in three classes: overstory white spruce; overstory aspen; and understory white spruce. Light measurements were made with a hand-held integrating radiometer (Sunfleck Ceptometer, model SF-80, Decagon Devices, Inc., Pullman, WA). The 80 cm long probe measures photosynthetically active radiation (PAR) simultaneously with 80 sensors. The internal microprocessor averages and stores any number of readings taken. Nine PAR readings were taken per tree, with three parallel readings taken in the top, middle and bottom of each crown's shadow. Trees with overlapping shadows were omitted. Measurements of total ambient PAR and ambient diffuse PAR were also taken with the radiometer in the open, at the beginning and end of each sampling period. Diffuse PAR was measured by shading the tip sensor with a 10 x 10 cm disc held 1 m away.

On a sunny day in late June 1994, 30 tree crowns were sampled during five time periods: 9:47 to 10:57; 11:42 to 12:30; 12:38 to 13:30; 15:12 to 16:10; and 16:48 to 17:53 solar time. The solar elevations (angle of the sun from the horizon) that relates to the midpoint of these time periods on our sampling day (June 21, 1994) were: 54.3°; 59.3°; 57.1°; 38.8°; and 24.7°. Due to the similarity in solar elevation between the first three sampling periods, data from these periods were combined and given the average solar elevation of 57°.

Ten of the trees of each type (overstory aspen, overstory white spruce, understory white spruce) were measured for total height, crown length (aspen only, crown length was equal to total height in white spruce), diameter at breast height (dbh), and crown radius in two directions. Crown radius of aspen was

estimated using a clinometer to find the distance from the bole to the outermost point of overhead foliation.

The diffuse component of ambient PAR was subtracted from both above and below canopy readings to give direct beam estimates. Tree level direct beam light transmission was then calculated as the average of the nine individual PAR readings taken per crown shadow, divided by the average direct beam PAR for that sampling period. A two-way analysis of variance (ANOVA) was conducted on percent light transmission, with multiple comparisons of means to further describe any significant differences found (Appendix II).

Vertical and horizontal crown areas were calculated from crown radii, and the length of the live crown. Overstory aspen crown area was calculated as an ellipsoid, understory white spruce crown area as a cone, and overstory white spruce crowns as a cone (1/3 of crown length) on top of a cylinder (2/3 of crown length). Crown shadow areas were estimated based on specific solar elevations, crown length, crown radii and assumed crown shape. First, crown shadow lengths were calculated based on a tangent function of solar elevation and crown length, then the shadow area cast on the ground was estimated from crown shadow length, crown radii and the chosen geometric shape. Correlations of crown characteristics based on dbh were made for white spruce and aspen. All statistical analyses were conducted with SAS version 6 (SAS Institute Inc., Cary, NC).

Results

The diffuse fraction of ambient PAR increased from 7.1 % at 57° solar elevation angle to 18.2% at 25°. Overstory aspen crowns transmitted

substantially more light than overstory white spruce crowns over all solar elevation angles sampled (Fig. III-1; Appendix II-c, $p < 0.05$). The aspen crowns transmitted the least light (17 %) at high solar elevations, and transmitted the most light (34 %) at a relatively low solar elevation. At a mid solar elevation angle (39°) aspen crowns transmitted similar light levels (19 %) as the higher solar elevations. Light transmission through the white spruce crowns followed the same general pattern as that for aspen, showing a steady increase from 4 % at high solar elevations to 11 % at the low solar elevation. The understory white spruce crowns transmitted light at levels between those of the overstory aspen and white spruce. The pattern followed was opposite that of the overstory white spruce, with a rapid rise in light transmission from the high to mid solar elevation and less increase from the mid to low solar elevation. At the mid solar elevation, there was little difference between light transmission through the overstory aspen crowns and the understory white spruce crowns due to the relatively low light transmission of aspen, and the relatively high light transmission of understory white spruce, for that solar elevation.

The crowns of overstory white spruce trees were mostly vertically distributed. Heights of 10 overstory white spruce ranged from 26 to 34 m, leading to a range in estimated vertical crown area from 121 to 215 m^2 (based on a rocket shape with 1/3 of total height in the cone, and 2/3 in the cylinder) (Table III-1). Mean crown radius ranged from 2.4 to 3.9 m for trees 43 to 80 cm in dbh. Horizontal crown areas based on these crown radii ranged from 17 to 48 m^2 (based on an ellipsoid).

The 10 understory white spruce trees sampled for crown size had a broad range in heights (5 to 21 m) and a narrow range in mean crown radius (1.2 to 3.2 m) (Table III-1). Their crown areas, based on a cone, showed a range of 6 to 66 m^2 in vertical area and 5 to 32 m^2 in horizontal area.

The crowns of the overstory aspen trees were distributed more evenly between the vertical and the horizontal. Trees ranged from 23.5 to 29 m in height, yet crowns were only 6 to 7.5 m long (Table III-1). Mean crown radii for trees 26 to 42 cm in dbh ranged from 1.6 to 3.0 m. Crown areas, based on an elliptical shape ranged from 15 to 32 m^2 in vertical area and 8 to 27 m^2 in horizontal area.

The shadow area cast by the crowns of selected overstory aspen, white spruce and understory white spruce were estimated in Fig. III-2 in relation to solar elevation. The high vertical distribution of the overstory white spruce trees resulted in much larger shadow areas than the smaller more evenly distributed aspen crowns, since solar elevation in this area is never greater than 60°. For example: two understory white spruce trees of 35 cm dbh had an average shadow area of 48 m^2 at 57° and an area of 132 m^2 at 25° solar elevation angle, whereas two aspen trees of the same dbh averaged only 23 m^2 at 57° and 59 m^2 at 25°.

There was a strong relationship between dbh and crown size variables of white spruce, but aspen showed only a poor correlation. Dbh was a good predictor of total height ($r^2 = 0.94$, $p<0.0001$), mean crown radius ($r^2 = 0.81$, $p<0.0001$), horizontal crown area ($r^2 = 0.78$, $p<0.0001$), and vertical crown area ($r^2 = 0.94$, $p<0.0001$) in understory and overstory white spruce ($n=20$; Fig. III-3). In contrast, aspen crown radius ($r^2=0.06$, $p>0.51$, $n=10$, data not shown) and crown length ($r^2=0.002$, $p> 0.91$, $n=10$, data not shown) were not predicted well by dbh.

Discussion

Light transmission through the crowns of individual aspen and white spruce trees increased with decreased solar elevation angle (Fig. III-1). Over all solar elevations, overstory white spruce transmitted substantially less light than either understory white spruce or overstory aspen. Based on the length and width of overstory white spruce crowns, crown area was largely distributed vertically (Table III-1). At high solar elevations, light has a longer path through the crown than at low elevations; hence more light is captured than at low elevation angles. Understory white spruce likely transmitted more light than overstory white spruce due to the decreased foliation held at the lower light levels found in the understory (O'Connell and Kelty 1994).

The crowns of overstory aspen have their leaf area distributed more evenly between the vertical and horizontal planes (Table III-1). One would therefore have expected the shade cast by aspen to be more independent of solar elevation. However, the leaf orientation of aspen causes the attenuation of light through aspen crowns to change (Jarvis and Leverenz 1983). Deciduous leaves are generally oriented more to a horizontal than to a vertical plane (Young 1985, Jarvis and Leverenz 1983). Even with a spherically shaped aspen crown, attenuation of light will still be far greater at high elevation angles than at low angles due to the orientation of the leaves. Our data also suggests that a more horizontal leaf angle distribution is controlling light transmission through aspen crowns, by the insignificant increase in light transmission between high and mid solar elevations and the large increase in light transmission at low solar elevations (Fig. III-1). When the incident solar beam nears the leaf angle orientation, light penetration is from the side of the leaves, where the least leaf area is projected for light capture. In contrast, the steady increase in light transmission with decrease in solar elevation angle in the overstory white spruce

crowns suggested a random (or spherical) leaf angle distribution rather than a specific leaf angle distribution. Light transmission through the understory white spruce suggests that crowns are oriented for maximum light capture at high solar elevations (O'Connell and Kelty 1994), since light transmission through their crowns is far lower at high elevation than mid or low solar elevations. Yet, at low densities in mixed stands, long crowns may be an advantage over short crowns.

The crowns of overstory aspen trees were small compared to those of overstory white spruce, especially in vertical area (Table III-1). White spruce and aspen shadow areas were closest in size at high elevation angles where crown radii determined how much shadow was cast. With decreasing solar elevation, the long white spruce crowns cast increasingly larger shadow areas than aspen. In general, the crown shape and leaf orientation of aspen caused less change in shadow area with solar elevation than overstory or understory white spruce (Fig 2). The larger shadow areas of white spruce combined with lower light transmission, result in a six-fold increase light interception compared to overstory aspen. The crown characteristics and shading potential of individual white spruce trees were well predicted from dbh or height measurements (Fig. III-3), while the crown characteristics of aspen crowns were not well predicted; partially due to a smaller sample size and narrower range in crown sizes, but also because the length of the live crown of aspen changes little after 15 - 20 years of age (Peterson and Peterson 1992). Johnstone and Peterson (1980) found a correlation between aspen stand leaf area index (LAI) and number of stems per hectare but not mean stand height.

In mixed stands, aspen and white spruce occupy different crown niches and have different strategies for capturing light. Aspen crown shape (an ellipsoid), with near horizontal leaf orientation is best suited to capture light at

high solar elevation angles in the late spring and summer, whereas conical or cylindrical white spruce crowns with a random leaf angle distribution are not as efficient at capturing light at high solar elevations, but project a large surface area at low solar elevations (Fig. III-2). The deciduous aspen make the most of high light conditions with high net assimilation rates (Peterson and Peterson 1992). White spruce can photosynthesize at lower light levels (Leverenz 1987) and may take advantage of light at lower solar elevation when deciduous aspen crowns are leafless in the autumn and spring (Chapter II).

Stand level light transmission shows a markedly different response to solar elevation than individual trees. Low solar elevation angles, found early and late in the day (Canham *et al.* 1994, Black *et al.* 1991, Hutchison and Matt 1977) or early and late in the growing season (Chapter II, Uemura 1994, Gholz *et al.* 1991, Ross *et al.* 1986) cause decreased rather than increased light transmission due to shading wood area. Canham *et al.* (1994) and Hutchison and Matt (1977) found the greatest light transmission through overstory canopies during solar noon which offered the highest solar elevations. The attenuation of light at lower solar elevations, through multiple layers of crowns and wood area, must then greatly decrease light transmission over what individual tree crowns predict. Kellomaki *et al.* (1984) suggest that the importance of crown shape decreases as stand density increases.

The results of this study show the high light intercepting capacity of individual white spruce trees and the low levels of light available beneath their crowns. Overstory white spruce was found to intercept six times as much light as overstory aspen. The strategies of each species to capture light were examined. Managers interested in increasing light transmission to the understory of boreal mixedwood stands should be aware of the overwhelming influence of white spruce crowns.

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Tree Type	Dbh (cm)	Total Height (m)	Crown Length (m)	Mean Crown Radius (m)	Vertical Crown Area (m2)	Horizontal Crown Area (m2)
S	42.97	26.0		3.0	130.00	28.27
S	57.30	31.0		2.4	121.42	17.35
S	57.61	30.0		3.4	167.50	35.26
S	70.03	31.0		3.2	165.33	32.17
S	70.03	34.0		3.5	198.33	38.48
S	71.62	33.0		3.9	214.50	47.78
S	72.26	32.0		3.1	162.67	29.22
S	73.21	33.0		3.7	203.50	43.01
S	74.80	32.0		3.0	160.00	28.27
S	79.58	33.0		3.9	214.50	47.78
uS	6.37	5.0		1.2	6.00	4.52
uS	8.59	7.9		1.4	11.06	6.16
uS	11.78	8.0		1.6	12.40	7.55
uS	18.46	13.0		1.7	22.10	9.08
uS	20.37	14.1		2.1	29.61	13.85
uS	23.24	17.5		2.3	40.25	16.62
uS	25.78	21.0		2.2	46.20	15.21
uS	31.19	20.0		2.0	40.00	12.57
uS	34.70	21.0		2.2	46.20	15.21
uS	35.01	20.5		3.2	65.60	32.17
A	25.46	23.5	6.0	1.6	14.61	7.55
A	28.01	26.0	7.0	2.2	23.64	14.52
A	28.97	23.5	6.5	2.0	19.91	11.95
A	29.28	25.0	7.0	1.9	20.89	11.34
A	32.47	24.5	6.5	1.9	18.89	10.75
A	33.42	24.0	7.0	3.0	32.44	27.34
A	33.42	26.0	7.5	2.4	27.69	17.35
A	34.70	29.0	7.0	2.2	23.64	14.52
A	35.01	28.0	7.0	2.2	24.19	15.21
A	42.02	26.0	6.0	1.9	17.91	11.34

Table III-1. Dbh (stem diameter at 1.3 m), height, and crown measures of ten overstory white spruce, S; understory white spruce, uS; and overstory aspen, A.

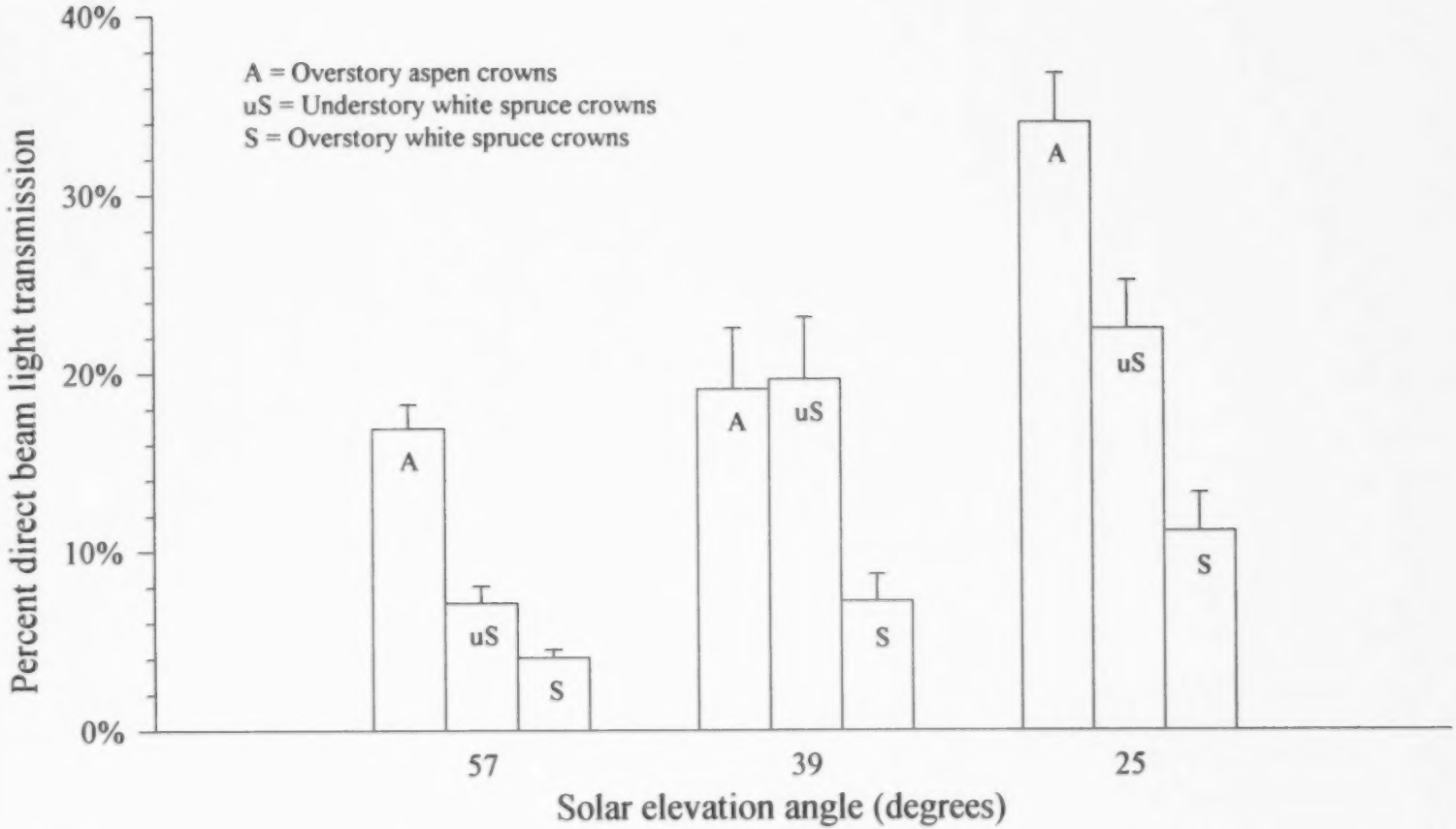

Fig. III-1. Average direct beam light transmission through individual crowns of overstory aspen, understory white spruce and overstory white spruce as related to three solar elevation angles (mean + standard error of the mean); n = 30 (57°), n = 10 (39° and 25°).

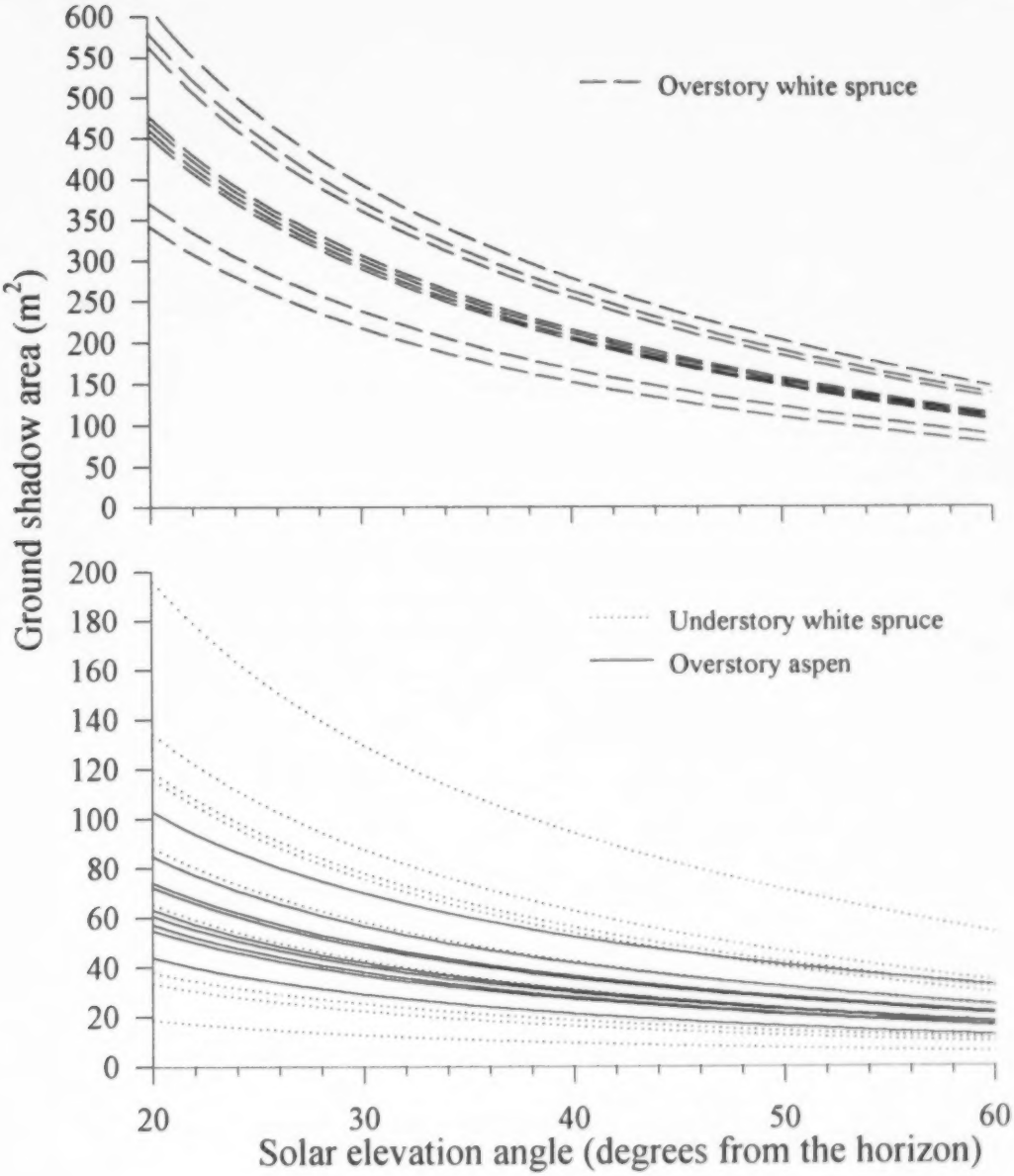

Fig. III-2. The change in shadow area of ten overstory white spruce, understory white spruce and overstory aspen with solar elevation. Shadow areas are based on geometric shapes: overstory white spruce, a rocket shape (1/3 of crown length as a cone, 2/3 as a cylinder); understory white spruce, a cone; and overstory aspen, an ellipsoid.

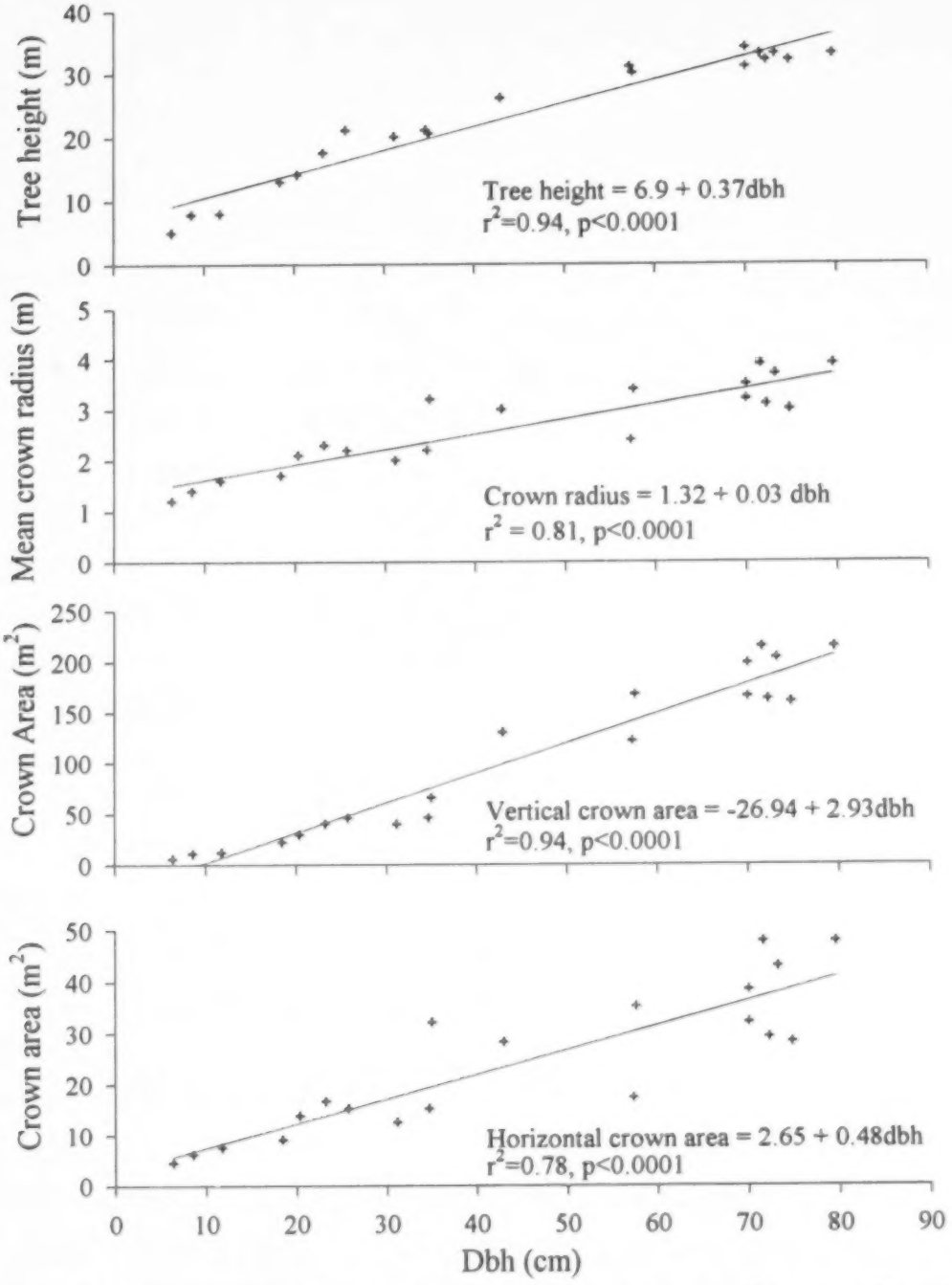
Tree height (m)
Tree height = 6.9 + 0.37dbh
r²=0.94, p<0.0001
Mean crown radius (m)
Crown radius = 1.32 + 0.03 dbh
r² = 0.81, p<0.0001
Crown Area (m²)
Vertical crown area = -26.94 + 2.93dbh
r²=0.94, p<0.0001
Crown area (m²)
Horizontal crown area = 2.65 + 0.48dbh
r²=0.78, p<0.0001
Dbh (cm)

Fig. III-3. Correlations of over- and understory white spruce dbh (stem diameter at 1.3 m) with a) total height; b) crown radius; c) vertical crown area; d) horizontal crown area (n = 30).

Chapter IV.

Discussion and Conclusions

There has been a resurgence of interest in using advance regeneration to decrease rotation time and regeneration costs in the boreal mixedwoods (Navratil *et al.* 1989, Brace and Bella 1988). Currently, attempts are made to protect advance white spruce regeneration during harvesting operations, but its development is left to chance. Seed sources, appropriate seedbeds, and light are some of the requirements necessary for white spruce to establish in the understory. In general, the light requirements of white spruce germinants and seedlings are known (Lieffers and Stadt 1994, Leverenz 1987, K. Greenway unpublished data, Brix 1972, Logan 1969). However, it is not known what light environments exist on the forest floor of boreal mixedwood stands of different composition and age.

The objective of the first study (Chapter II) was to quantify light penetration to the forest floor of boreal mixedwood stands as affected by over- and understory canopies in the spring, summer and autumn. Light transmission was measured through three overstory types (pure young aspen, pure old aspen and mixed old aspen-white spruce stands) at three height levels: below the overstory canopy, 1.3 m; below the shrub canopy, 0.5 m; and on the ground below the herb layer. In the summer, increased light transmission through the overstory resulted in increased light interception by the understory layers. As a result, light levels on the forest floor in the summer were equally low in all overstory types. The light levels found in the summer support a theoretical relationship proposed by Cannell and Grace (1993) of increasing understory leaf area index (LAI) with decreasing overstory LAI. In the summer, light levels on the forest floor were barely above the photosynthetic compensation level for white spruce.

Seasonally, the pure aspen stands showed large differences in light transmission, with light intensities well above the photosynthetic saturation level for white spruce reaching the understory in the spring. The least light was available in the summer, and intermediate light intensities reached the understory in the autumn. In contrast, the mixed aspen-white spruce stands showed a decrease from the highest light intensities in the spring to very low levels in the autumn. However, even the highest light intensities were well below photosynthetic saturation levels for white spruce. The pure aspen stands transmitted far more light than the mixed aspen-white spruce stands in the spring and autumn due to lack of deciduous cover in the over- and understory. Autumn light levels were less than those found in the spring due to the greater shading of crowns and boles at the relatively low solar elevations. These results suggest that white spruce advance regeneration may rely on high light conditions during the deciduous leaf-off period in the autumn, and particularily in the spring, for a large portion of their annual carbon gain. Since the shading capacity of white spruce is much greater than aspen in the spring and autumn, the amount of white spruce in the overstory is likely the most important factor in determining the amount of light transmitted to white spruce advance regeneration. In a study of similar stand types, Lieffers and Stadt (1994) found that increased basal area of softwoods to decrease light transmission, and increased basal area of hardwoods increased light transmission. No meaningful relationship has been determined for total basal area of mixed stands and light transmission for fully-leafed summer conditions or for the hardwood leaf-off periods in the spring and autumn. In order to clarify the role of aspen and white spruce with regard to light transmission to the understory of mixedwood stands, a second study was undertaken.

The objectives of the second study (Chapter III) were to quantify the differences between individual aspen and white spruce crowns in size, light

transmission and capacity to shade. Percent direct beam transmission through ten overstory white spruce, aspen and understory white spruce were measured over three solar elevation angles (57°, 39°, and 25°) in midsummer. Crown areas were calculated based on crown measurements and assumed geometric shapes: overstory white spruce as a cone (1/3 of crown length) on top of a cylinder (2/3 of crown length); overstory aspen as an ellipsoid; and understory white spruce as a cone. Overall, light transmission increased with decreased solar elevation angle. This is contrary to what is found in closed stands of the same species (Chapter II, Ross *et al.* 1986), likely due to the increase in crown and bole shading area with decreased solar elevation. Aspen crowns were much smaller and transmitted more light than overstory white spruce crowns. Understory white spruce exhibited a broad range in crown sizes and transmitted less light than overstory white spruce; likely due to decreased foliation (O'Connell and Kelty 1993). With decreasing solar elevation, white spruce crowns cast increasingly larger shadow areas than aspen. Large shadow areas combined with lower light transmission cause white spruce to have an overwhelming shading effect (about six times as much as aspen) in mixed stands.

These studies in conjunction with others in the boreal mixedwoods: light transmission and growth of understory competitors with white spruce (Lieffers and Stadt 1994, Lieffers *et al.* 1993); understory white spruce photosynthesis in the spring and autumn (R. Man and V. Lieffers unpublished); understory seedbed requirements (H. DeLong and V. Lieffers unpublished); silvicultural and harvesting systems to protect understory white spruce (Navratil *et al.* 1994, Froning 1980); and windthrow protection of residual overstories (Navratil *et al.* 1994); lead to increasing sophistication of a two-stage harvesting/silvicultural system that promotes advance

regeneration of white spruce during the aspen rotation as described by Navratil *et al.* (1989). The information that remains lacking for managers to implement such a system, is how much overstory of which species to cut in order to achieve: the appropriate amount of understory light for advance regeneration; protection from frost and high summer temperatures; and windfirmness of the overstory. As seen earlier, aspen and white spruce have very different capacities to intercept and transmit light. The difficulty in providing light information is the great variety of overstory compositions found in the boreal mixedwoods, and the inverse relationship between basal area and light transmission between white spruce and aspen (Lieffers and Stadt 1994). The amount of empirical data necessary to cover all stand compositions and overstory removal intensities is too immense to undertake. What is required is a simple model predicting light transmission by the proportion and density of aspen to white spruce in basal area. Before such a model can be developed the relationship between basal area and the very different crown characteristics of aspen and white spruce must be identified. In Chapter III, dbh (stem diameter at 1.3 m) was found to be a good predictor of tree height and crown radius in white spruce, but not in aspen. It remains difficult to predict aspen crown sizes at the old ages which are typically found in mixtures with white spruce. Further, a light transmission model to predict light penetration to the forest floor must include: the relationship between overstory light transmission and understory cover in the summer; wood shading area in the spring and autumn; and the effects of site quality, live crown ratios and stand densities.

The studies presented provide preliminary empirical data on the light transmission and light intercepting capacity of individual white spruce and aspen, and on the amount of light available above and below the understory in three different boreal mixedwood overstory types.

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Appendix I.

(a)
ANOVA Table - Split Plot Design
Effect of Overstory Type, Season, and Height Level on % Light Transmission

Source	DF	Mean Square	F Value	P Value
Overstory Type	2	5960.03	25.88	0.0001
Site /Type	15	4016.50	n/a	n/a
Season	2	9925.56	194.12	0.0001
Season x Type	4	1203.88	23.54	0.0001
Season x Site/Type	21	51.13	n/a	n/a
(Height) Level	2	2464.06	343.30	0.0001
Type x Level	4	285.69	39.8	0.0001
Season x Level	4	32.67	4.55	0.0025
Season x Type x Level	8	35.04	4.88	0.0001

(b)
Multiple Comparisons
Season and Height Level Interactions, P values, alpha = 0.05

	Height Levels		
Seasons	**0 - 0.05 m**	**0.5 m**	**1.3 m**
Spring	<0.0001	<0.0001	<0.0001
Summer	0.5477	0.0223	0.0009
Autumn	0.0037	0.0061	0.0041

Appendix II.

(a)
ANOVA Table
Effect of Solar Angle and Tree Type on Light Transmission

Source	DF	Mean Square	F Value	P Value
Solar Angle	2	2052.8	43.6	0.0001
Tree type	2	2453.4	52.15	0.0001
Solar Angle x Tree type	4	230.5	4.9	0.0010

(b)
Multiple Comparison of Light Transmission Means
Least Significant Difference (LSD), P values, alpha = 0.05

Solar Angle	25	57	39
25	n/a	0.0001	0.0001
57	0.0001	n/a	0.0001
39	0.0001	0.0001	n/a

(c)
Multiple Comparison of Light Transmission Means
Least Significant Difference (LSD), P values, alpha = 0.05

Tree type	Aspen	White spruce	Understory white spruce
Aspen	n/a	0.0001	0.0001
White spruce	0.0001	n/a	0.0001
Understory white spruce	0.0001	0.0001	n/a